THE PHYLOGENY AND CLASSIFICATION OF THE ZINGIBERALES[1]

W. John Kress[2]

ABSTRACT

In the Zingiberales, a primarily tropical order of monocotyledons, most phylogenists currently recognize eight families: Musaceae, Strelitziaceae, Lowiaceae, Heliconiaceae, Zingiberaceae, Costaceae, Cannaceae, and Marantaceae. Some taxonomists still prefer the earlier classifications that included Strelitziaceae, Lowiaceae, and Heliconiaceae in Musaceae s.l., and Costaceae as a part of Zingiberaceae s.l. Attempts to reconstruct the phylogenetic history of the order have been made by Lane, Tomlinson, and Dahlgren & Rasmussen. An original analysis of the evolutionary relationships of the eight families of the Zingiberales based on the principles of phylogenetic systematics is presented here. The most parsimonious topology is (Musaceae (Strelitziaceae (Lowiaceae (Heliconiaceae ((Zingiberaceae, Costaceae) (Cannaceae, Marantaceae))). The cladogram rejects the recognition of Musaceae s.l. as an evolutionary group. A new phylogenetic classification based on the cladogram is proposed that recognizes eight families, two superfamilies, and five suborders within the Zingiberales.

"The Scitamineae [Zingiberales] is a very natural order of monocotyledons, somewhat comparable in its homogeneity to grasses, palms or orchids. . . , long recognized by taxonomists as a natural entity" (Tomlinson, 1962).

"The Order Zingiberales is well characterized and sharply defined; its limits have occasioned no controversy . . . . One could wish that the families in all orders were as well marked and sharply defined as those in the Zingiberales" (Cronquist, 1981).

"The Zingiberiflorae, whether treated as a separate superorder, as here, or an order in a more widely circumscribed unit, is one of the most indisputably natural suprafamilial groups" (Dahlgren, Clifford & Yeo, 1985).

The Zingiberales, or Scitamineae, are a group of monocotyledons whose members are almost entirely restricted to tropical regions. As indicated by the above quotations, the order is widely accepted by most taxonomists and phylogenists to be a distinctly circumscribed "natural" or monophyletic lineage of plants. No morphological characters are in conflict with the acceptance of the Zingiberales as a monophyletic group.

In a brief diagnosis of the morphological and anatomical characters that distinguish the order, Tomlinson (1962) included the following: rhizomatous herbs; leaves with open, sometimes ligulate sheaths; lamina entire with lateral veins diverging from a common midrib, one-half of blade completely rolled around the other during development; hairs commonly unicellular; guard cells each with two narrow lateral subsidiary cells parallel to the pore; hypodermis of colorless cells below each surface of lamina; air canals in leaf axis segmented by transverse diaphragms containing stellate cells; leaf axis with a single main arc of large vascular bundles and subsidiary systems of smaller bundles; silica cells or stegmata associated with vascular bundles in all parts except roots; inflorescence terminal or lateral, commonly racemose with conspicuous bracts; flowers (Fig. 1) zygomorphic, perianth consisting of separate calyx and corolla; fertile stamens usually five or one; one to five stamens usually represented by staminodes; ovary inferior, three-locular, with one to many ovules in each locule; seeds with abundant endosperm, often arillate.

In reviewing these characters and subsequently studied features, Dahlgren and coworkers (1985) listed six apomorphies for the Zingiberales (their

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Superorder Zingiberiflorae): root hair cells shorter than other epidermal cells, sieve tube plastids containing starch, presence of silica bodies, epigynous flowers, lack of distinctive apertures on the pollen grains, and the occurrence of arillate seeds. Although some of the features vary within families, these uniquely derived states distinguish the Superorder Zingiberiflorae from its closest relatives in the monocotyledons. However, for most botanists it is the herbaceous arborescent stem, the distichous phyllotaxy, the large petiolate leaves with blades possessing transverse venation, the conspicuous, colorful bracteate inflorescences, and the substitution of one to five staminodia for the fertile stamens that distinguish the Zingiberales as a homogeneous and natural group.

The distinctiveness of the Zingiberales has caused controversy in determining the relationship of the order to other monocotyledons. Based on similarity in inflorescence and flower structure (primarily the large, conspicuous bracts and petaloid perianths) most modern phylogenists have agreed that the Zingiberales and Bromeliales (containing the single family Bromeliaceae) have shared a most recent common ancestor (Hutchinson, 1973; Stebbins, 1974; Takhtajan, 1980; Cronquist, 1978, 1981; but see Thorne, 1976, and Walker, unpublished). Although the homologies of the inflorescence bracts and perianths are not unequivocal, several possibly unique chemical characters (myricetin and/or quercitin glycosides) shared by the two orders also suggest a common ancestor (Williams & Harborne, 1977). Based on the presence of the conspicuous petaloid perianth, Dahlgren et al. (1985) have hypothesized the Zingiberales as the sister group to their larger taxon Bromeliiflorae, which includes the Bromeliaceae, Velloziaceae, Philydraceae, Haemodoraceae, Pontederiaceae, Sparganiaceae, and Typhaceae. Until contrary evidence becomes available, the Bromeliales serve as the best outgroup to the Zingiberales in the monocotyledons.

The common ancestor of the Zingiberales–Bromeliales lineage (Zingiberidae of Cronquist) and other monocots is even more unclear. The presence of two distinctive perianth whorls of sepals and petals that may coalesce but never fuse and the presence of starchy endosperm are shared with a Commelinalian ancestor (Hutchinson, 1973). The septal nectaries, vessels primarily in the roots, and several chemical characters (e.g., chelidonic acid) ally the Zingiberales to the Lilialian lineage (Takhtajan, 1980). Dahlgren et al. (1985) have shown that starchy endosperm, epicuticular wax of the *Strelitzia* type, UV-fluorescent organic acids in the cell walls, and two or four subsidiary cells in the stomatal complex are apomorphies of the Zingiberiflorae–Bromeliiflorae–Commeliniflorae lineage. These last characters provide the best evidence for accepting a common ancestry with a Commelinalian line. However, Walker (1987) has chosen to derive his Zingiberidae (excluding the Bromeliales), and its sister group, the Pontederiidae (Haemodoraceae, Pontederiaceae, and Philydraceae), directly from a primitive Liliid lineage.

HISTORY OF THE CLASSIFICATION OF THE ZINGIBERALES

The history of the classification of the Zingiberales, like many tropical plant groups, is one of continual refinement and division (Table 1). Bentham & Hooker (1883) recognized four tribes in their Ordo (Family) Scitamineae: Zingibereae, Maranteae, Canneae, and Museae. These tribes were delineated by the degree of fusion of the perianth parts, the number of fertile stamens and staminodes, the number of locules per anther, the style and stigma type, the number of ovules per locule, and the shape of the embryo (Fig. 1). Petersen (in Engler & Prantl, 1889) raised the rank of the four tribes to family and subdivided the Musaceae, which was held together primarily by the number of fertile anthers, into the tribes Museae (containing *Musa*, *Ravenala*, and *Strelitzia*) and Heliconieae (*Heliconia*). The solitary ovule per locule, septicidal fruit dehiscence, and inverted symmetry of the flowers distinguished *Heliconia* from the other members of the Musaceae. *Orchidantha*, the sole genus in the Lowiaceae, was excluded from the Scitamineae of Bentham & Hooker, but recognized as a possible member of the group by Petersen.

Schumann in *Das Pflanzenreich* (in Engler, 1900, 1902, 1904) further subdivided the Order Scitamineae by segregating genera into subfamilies. In the Zingiberaceae, the Costoideae was recognized as distinct from the Zingiberoideae on the basis of the spiral phyllotaxy and lack of essential oils in the former. The Musoideae (*Musa*), Strelitzioideae (*Strelitzia*, *Ravenala*, and *Heliconia*), and the Lowioideae (*Orchidantha*) were given subfamilial rank in the Musaceae. Here, *Heliconia*, *Strelitzia*, and *Ravenala*, possessing distichous phyllotaxy and hermaphroditic flowers, were separated from *Musa*, which possesses spirally arranged vegetative parts and unisexual flowers. Further subdivision separated the Strelitzioideae into the Strelitzieae (*Strelitzia* and *Ravenala*), with multiovulate locules and arillate seeds, from the Heliconieae (*Heliconia*), with uniovulate locules and no arils.

TABLE 1. Systems of classification of the Zingiberales.[1]

Bentham & Hooker (1883)	Petersen (Engler & Prantl, 1889)	Schumann (Engler, 1900, 1902, 1904) Winkler; Loesener (Engler & Prantl, 1930)
Family: Scitamineae	No rank	Order: Scitamineae
Tribes	Families	Families
Museae	Musaceae	Musaceae
(*Musa, Ravenala, Strelitzia, Heliconia*)	Tribes	Subfamilies
	Museae	Musoideae
	(*Musa, Ravenala, Strelitzia*)	(*Musa*)
		Strelitzioideae
		Tribes
		Strelitzieae
		(*Strelitzia, Ravenala*)
		Heliconieae
		(*Heliconia*)
		Lowioideae
	Heliconieae	
	(*Heliconia*)	
Zingibereae	Zingiberaceae	Zingiberaceae
		Subfamilies
		Zingiberoideae
		Costoideae
Maranteae	Marantaceae	Marantaceae
Canneae	Cannaceae	Cannaceae

Hutchinson (1934, 1959, 1973), who used the ordinal name Zingiberales (after Nakai, 1941), accepted the divisions of Schumann, but raised to the rank of family the Strelitziaceae (including *Heliconia*) and Lowiaceae. He also further subdivided the Zingiberaceae into four tribes of equal status.

In most modern taxonomic treatments of the Zingiberales, eight families are recognized: Zingiberaceae, Costaceae, Marantaceae, Cannaceae, Musaceae, Strelitziaceae, Heliconiaceae, and Lowiaceae (Table 1). Nakai (1941) first suggested that the Costoideae and the Heliconieae be raised to family rank. The nonaromatic vegetative body,

spirally arranged leaves, and anther appendages were cited by Nakai as separating the Costaceae from the Zingiberaceae. The uniovulate locules, exarillate seeds, and capitate stigmas of the Heliconiaceae distinguished that taxon from the other families of the order. Subsequently Tomlinson (1962, 1969), in his investigations of the anatomy of the order, pointed out that the degree of morphological and anatomical differences among the eight entities is about the same (see also above quote by Cronquist), and therefore accepted the classification of Nakai. Stebbins (1974), Takhtajan (1980), Cronquist (1978, 1981), and Dahlgren and

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TABLE 1. Continued.

Hutchinson (1934, 1959)	Nakai (1941); Tomlinson (1962); Takhtajan (1980); Cronquist (1981); Dahlgren et al. (1985)	Kress[2]
Order: Scitamineae (later Zingiberales)	Order: Zingiberales	Order: Zingiberales
		Suborders Musineae Family
Families Musaceae (*Musa*)	Families Musaceae (*Musa, Ensete*)	Musaceae (*Musa, Ensete*)
		Strelitzineae Family
Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum, Heliconia*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum*)
		Lowineae Family
Lowiaceae	Lowiaceae	Lowiaceae Heliconineae Family
	Heliconiaceae (*Heliconia*)	Heliconiaceae (*Heliconia*) Zingiberineae Superfamilies Zingiberareae Families
Zingiberaceae Tribes Zingibereae Hedychieae Globbeae	Zingiberaceae	Zingiberaceae
Costeae	Costaceae	Costaceae Cannariae Families
Marantaceae	Marantaceae	Marantaceae
Cannaceae	Cannaceae	Cannaceae

[1] After Tomlinson (1962) and Kress (1984).
[2] See Table 5.

coworkers (1983, 1985) have followed Nakai and Tomlinson in the recognition of eight families in the order.

The changes in family concepts within the Zingiberales during the last hundred years can be attributed in part to an increased understanding over time of character distribution within the taxa. In the early classifications of the 1800s comparatively little was known about the number of taxa and the amount of character variation within each group. Hence, similarities among the taxa were stressed in devising classifications, as it was easier to fit new taxa into fewer categories. As more genera and species were discovered and described, discontinuities in character variation became more obvious and differences separating taxa became more apparent. The current recognition of eight families within the order is a direct result of the much larger data base of taxa and character distribution available today. An even further division of families may occur as additional data become available.

Phylogenists who have studied the Zingiberales have been mostly concerned with the degree of

character differences between families. The question of the monophyly of the taxa themselves has not been adequately addressed, i.e., the families have been defined in terms of grades and not clades. For example, if the Strelitziaceae of Hutchinson (including Heliconiaceae; 1934, 1959) or Loesener's Zingiberaceae (including Costaceae; in Engler & Prantl, 1930) are not monophyletic groups, then support is provided for the recognition of equal taxonomic status for the included families. However, if these larger taxonomic groups are descendents of a unique common ancestor (monophyletic), then the taxonomic status of each group becomes more of a practical matter than a phylogenetic one.

In this paper, the eight families of Nakai and Tomlinson are accepted as working hypotheses of monophyletic groups within the Zingiberales. Evidence from the cladistic analyses of the order (provided below) is used to test hypotheses on family boundaries.

THE FAMILIES OF THE ZINGIBERALES

Detailed descriptions of each of the eight families of the Zingiberales have been provided in several recent publications (Tomlinson, 1969; Cronquist, 1981; Dahlgren et al., 1985) and will not be repeated here. Those family characteristics pertinent to this discussion, including autapomorphies, are given below (also see Fig. 1).

FAMILY MUSACEAE A. L. JUSSIEU (1789)

The two genera of the Musaceae, *Musa* (35 species) and *Ensete* (seven species), are restricted to the Paleotropics of Africa, eastern Asia, Australia, and the South Pacific. The lacticifers, specialized laminal mesophyll with vasculated and nonvasculated parenchymatous septa, spirally arranged phyllotaxy, unisexual flowers, and baccate fruits distinguish the members of the Musaceae from other Zingiberales.

The commercial importance of bananas has always focused attention on this family, especially the parthenocarpic hybrid triploids. *Ensete*, formerly included within *Musa*, differs in its monocarpic habit, the presence of warty exinous protuberances on the pollen grain surface, the large seeds, and the "T-shaped" embryo.

FAMILY STRELITZIACEAE HUTCHINSON (1934)

The three genera and seven species of the family, *Strelitzia* (five species), *Ravenala* (one species), and *Phenakospermum* (one species), are restricted to southern Africa, Madagascar, and South America, respectively. Nakai (1941) erected a new genus *Musidendron*, not recognized by most taxonomists, for the members of *Phenakospermum* possessing a ligneous trunk, sessile inflorescence, differently colored bracts and flowers, and 8–12 rows of ovules per locule. Information on the geographic variation of *Phenakospermum* is insufficient at this time to evaluate adequately the validity of this segregate genus (Kress, unpublished). Unique features of the Strelitziaceae are the woody trunk (lost in some members of *Strelitzia*), the three free sepals, the two fused petals that enclose the five (or six in *Ravenala*) fertile stamens (Fig. 1), and the woody, loculicidal capsular fruit.

The close relationship of these three genera has been accepted by most authors (but see Lane, 1955). Early taxonomists included the Strelitziaceae in a broadly circumscribed Musaceae but often recognized it at some subfamilial ranking. On the basis of the distichous phyllotaxy and hermaphroditic flowers, Hutchinson (1934, 1973), deemphasizing the specialized features that set the genus apart, included *Heliconia* in his Strelitziaceae.
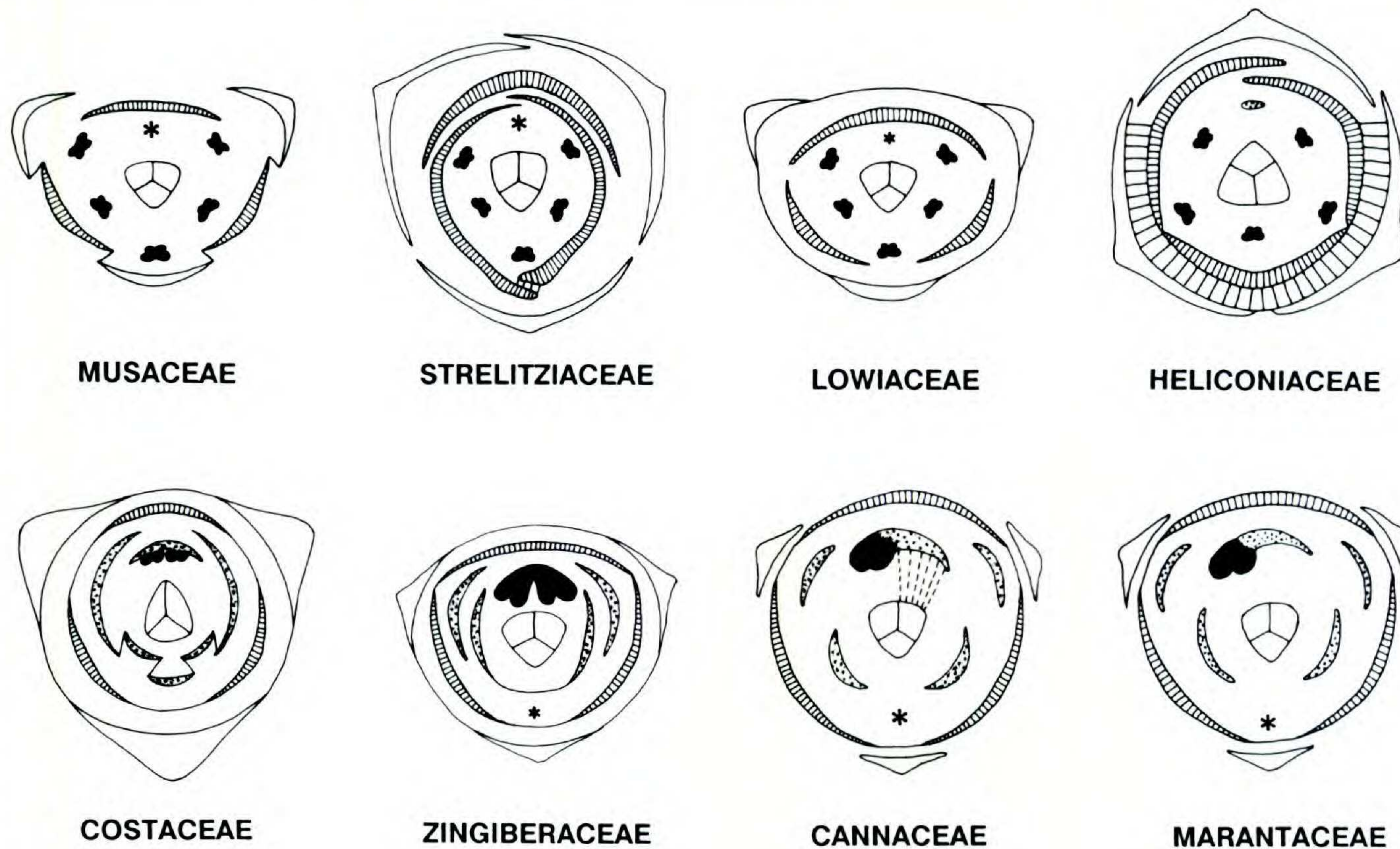
FAMILY LOWIACEAE RIDLEY (1924)

The single genus of the family, *Orchidantha*, with five to eight species, is found in Southeast Asia and some Pacific islands. The specialized leaf blade with mesophyll of irregularly arranged large and small cells (Tomlinson, 1962), several pairs of longitudinal veins parallel to the distinct midrib (Lane, 1955; Hutchinson, 1973), and the elaboration of the adaxial petal into a large labellum are among the obvious autapomorphies of the family.

Orchidantha has always been considered an unusual member of the Zingiberales and is most commonly classified either as a subfamily of or a separate family allied to the Musaceae. Lane (1955) accepted the Lowiaceae and stated that they are "probably as close to the Marantaceae or Zingiberaceae as to the Musaceae." No other phylogenists have accepted Lane's ambiguous placement of the family. The Lowiaceae are among the most poorly known taxa in the order in terms of taxonomy, general morphology, embryology, chemistry, and ecology.

FAMILY HELICONIACEAE NAKAI (1941)

The single genus *Heliconia* has perhaps 250 species that are distributed primarily in the Neotropics. Six species (at one time segregated as the genus *Heliconiopsis* Miquel) are found in the South Pacific from Samoa westward to Indonesia (Kress, 1990). The inverted symmetry of the flowers (the median sepal is adaxial in *Heliconia*), the presence of a single staminode opposite the un-

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FLORAL DIAGRAMS OF THE FAMILIES OF THE ZINGIBERALES

MUSACEAE STRELITZIACEAE LOWIACEAE HELICONIACEAE

COSTACEAE ZINGIBERACEAE CANNACEAE MARANTACEAE

◯ = SEPAL ▥ = PETAL ● = FERTILE STAMEN ⦿ = STAMINODE ✳ = ABSENT STAMEN

FIGURE 1. Floral diagrams of the eight families of the Zingiberales. For variable characters (e.g., stamen and staminode number) the most common state of the family is indicated. (Not drawn to scale; based on Lane (1955), Maas (1972), Kirchoff (1983a), and Kress (unpublished).)

paired sepal (Fig. 1), the heteropolar pollen grains, a single ovule per locule, and the drupelike fruits are autapomorphies of the family.

Heliconia has been variously associated with the Musaceae and the Strelitziaceae, depending upon the importance placed on the distichous phyllotaxy and hermaphroditic flowers (then placed with the Strelitziaceae) versus the terminal inflorescence, partial fusion of the calyx and corolla, and exarillate seeds (then placed with the Musaceae). Currently most taxonomists accept Nakai's placement of the genus in its own family Heliconiaceae.

FAMILY ZINGIBERACEAE LINDLEY (1835)

The Zingiberaceae, the largest family in the Zingiberales, consist of approximately 50 genera and 1,000 species. Their distribution is pantropical but concentrated in the Old World, especially in Southeast Asia. Because of the ephemeral flowers, taxonomic study of the family is difficult and a classification is still incomplete. The family has been variously divided into a number of tribes. Burtt & Smith (1972) recognized four tribes: Hedychieae, Zingibereae, Alpinieae, and Globbeae. The fusion

of the lateral staminodes of the inner staminal whorl into a labellum (Fig. 1), the presence of two epigynous nectariferous glands at the base of the style, and the occurrence of cells containing essential or ethereal oils are autapomorphies of the family. Other floral characters normally associated with the Zingiberaceae, such as the presence of a single fertile tetrasporangiate anther and the slender style, which lies between the two pollen sacs, are derived characters shared with the Costaceae, hence are not apomorphic in the family.

The Zingiberaceae have always been considered a natural group within the Zingiberales, with or without the Costaceae (see below). The reduction of the number of fertile pollen-bearing stamens to one, and the modification of the other stamens into petaloid staminodes, is a characteristic "trend" in the order and is carried to an extreme in the Marantaceae and Cannaceae.

FAMILY COSTACEAE NAKAI (1941)

The Costaceae, consisting of four genera and about 150 species, are distributed pantropically. The largest genus, *Costus* (100 species), is most

diverse in the Neotropics and is also found in Africa, Asia, and northern Australia. *Monocostus* (one species) and *Dimerocostus* (two species) are restricted to the New World tropics. *Tapeinochilos* (20 species), the most poorly understood genus in the family, extends through New Guinea, Indonesia, and tropical Australia. The well-developed (sometimes branched) aerial stem, distinctive staircaselike spirally arranged phyllotaxy, fusion of the five staminodes into a labellum (Fig. 1), petaloid filament and connective, and distinctly aperturate acetolysis-resistant pollen grain wall are characters unique to the Costaceae. The multicellular trichomes and the poorly developed system of air canals in the leaf axis (Tomlinson, 1962) may also be autapomorphies.

The Costaceae were at first always classified as a subdivision of the Zingiberaceae, either as a subfamily or tribe. Nakai's (1941) suggestion that the Costaceae deserved familial rank was supported by Tomlinson's (1962) anatomical investigations and has been accepted by many recent phylogenists. Early taxonomists united the two families on the basis of several inflorescence and floral characters (see above under Zingiberaceae), which as Tomlinson (1962) pointed out, "may indicate evolution from a common ancestor, yet total differences between them warrant independent familial rank."

FAMILY CANNACEAE A. L. JUSSIEU (1789)

Canna, the solitary genus in the family, is primarily found in the New World tropics and subtropics. The pantropical distribution of *C. indica* is most likely the result of human dispersal. Estimates on the number of species in *Canna* range from 9 to 50 (Segeren & Maas, 1971; Maas, unpublished). The presence of mucilage cells and a petaloid style fused to the single fertile stamen (Fig. 1) are the most obvious autapomorphies of the family. Many other features that readily distinguish the Cannaceae from the other families of the order, such as the asymmetric flowers, reduction of fertile anthers to a single bisporangiate anther sac, and secondary pollen presentation, are shared with the Marantaceae.

The Cannaceae have been recognized by all taxonomists as a distinct taxonomic entity, usually at the family level within the Zingiberales. The morphological similarities with the Marantaceae have invariably led to the close placement of the Cannaceae with that family in all classifications proposed.

FAMILY MARANTACEAE PETERSEN IN ENGLER & PRANTL (1889)

The Marantaceae are the second-largest family in the order, with 30 genera and 450–500 species. Although the geographic distribution is pantropical, three-quarters of the species, many in the large genus *Calathea*, are found in the Neotropics. The classification of the family is still inadequately resolved with no general consensus on subfamilial divisions (Andersson, 1981; H. Kennedy, pers. comm.). Apomorphies of the family include the leaf pulvinus, sigmoid lateral veins and evenly spaced cross-veins of the leaf blade, terminal enantiomorphic pairs of flowers, two inner staminodes (cucullate and callous staminodes, which are modified into structures for the explosive release of the pollen at pollination), and the single ovule per locule.

As with the Cannaceae, all phylogenists have agreed upon the separate familial status of the Marantaceae. Based on the highly modified zygomorphic flowers and the reduction in the number of fertile pollen-bearing stamens to a single bisporangiate pollen sac, most taxonomists consider the Marantaceae to be the most derived family of the Zingiberales.

PAST PHYLOGENETIC INVESTIGATIONS OF THE ZINGIBERALES

FOSSIL EVIDENCE

In some cases fossils may provide information on the evolutionary history of a plant group. For the Zingiberales, fossil records have been attributed to five of the eight families. Most of the fossil specimens have been collected in Eocene deposits. Eocene fruits of the fossil taxa *Musa cardiosperma* have been found in India (Jain, 1963; Daghlian, 1981). Various vegetative structures found in the same Deccan Intertrappean beds of India have been tentatively assigned to the Heliconiaceae (Trivedi & Verma, 1971). Leaf specimens of the genus *Musophyllum* found in neotropical Tertiary beds also have been attributed to *Heliconia* (Berry, 1921; Simmonds, 1962). The oldest fossils of the order are leaves of the Zingiberaceae in the fossil genus *Zingiberopsis* from the late Cretaceous (Hickey & Peterson, 1978). Ginger fruits and arillate seeds of the fossil *Spirematospermum* are well represented in Eocene through Miocene sediments of Denmark (Friedrich & Koch, 1970, 1972; Koch & Friedrich, 1971). Fossil leaves from the Eocene of Texas attributable to a possibly extinct genus of the Cannaceae have been reported by Daghlian

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(1982). Eocene deposits from England have yielded fossils resembling the leaves of the Marantaceae (Cronquist, 1981). Wodehouse (1932) suggested that fossil pollen of the Musaceae and Cannaceae occur in the Eocene Green River Flora of the western United States. However, the fragile, ace-tolysis-susceptible nature of the pollen wall of the Zingiberales, which would not stand up to normal processes of fertilization, makes this report suspect. No fossil records of the Strelitziaceae, Lowiaceae, or Costaceae have been reported.

The reports of fossil remains of the Zingiberales do not shed much light on the historical relation-ships of the families. Recognizable "gingers" ap-peared by the late Cretaceous and most of the families apparently had differentiated by the early Tertiary. The distinctive venation of the leaves of the Zingiberales has been important in allowing fossil taxa to be assigned to particular families (Hickey & Peterson, 1978). However, the lack of fossil flowers has prevented any paleontological in-terpretations of the evolution of the reproductive structures in the order.

PREVIOUS PHYLOGENETIC ANALYSES

Most classifications of the Zingiberales (Table 1) can be interpreted as a statement on the evolu-tionary relationships of the taxa. For example, the close relationship, at least morphologically, of the Cannaceae and Marantaceae was implied by the association of these two families in all classifica-tions. The broad interpretation of the Musaceae (sometimes excluding *Orchidantha*) to include all genera with five or six stamens likewise was a statement on the evolutionary "closeness" of those taxa. The same is true of the consistent classifi-cation of the Zingiberaceae–Costaceae complex. However, explicit statements on the actual phy-logenetic history of the order are few, especially in terms of sister-group relationships.

The first diagrammatic representation of the re-lationships of the groups within the Scitamineae (Fig. 2) was applied in the frontispiece of a book on bananas by Reynolds (1927). Although Reyn-olds did not explain or justify his illustration, the morphological similarities and perhaps evolutionary associations among the taxa of the closest relatives of *Musa* are depicted: similar taxa share a common branch or "sympodium" of the vegetative axis, thereby representing the genealogical history of the order.

Lane's analysis. Lane (1955), the first to consider

in detail the relationships within the Zingiberales, was most concerned with the taxa of the Musaceae s.l. Based on the reduced ovule number, flower orientation, and anatomical structure of the root, he believed the genus *Heliconia* to be the most derived member of the family. The similarities to *Musa* (terminal inflorescence, lack of aril, baccate fruit, and similar vegetative habit) led him to state that these two families "have been derived togeth-er, from a stock early divergent from the rest of the family . . . ." He also believed that *Strelitzia* and *Phenakospermum* are more closely related to each other than either is to *Ravenala*, which he considered the least derived genus of the family. Lane provided a classification of the Musaceae that included two subfamilies and three tribes based on these relationships. The subfamily Musoideae was made up of the tribe Ravenaleae (*Ravenala*), tribe Strelitzieae (*Strelitzia* and *Phenakospermum*), and tribe Museae (*Musa* and *Ensete*). The second subfamily, Heliconioideae, contained only the ge-nus *Heliconia*. In a cladistic sense Lane's classi-fication is difficult to reconcile with his statements on relationships, i.e., *Heliconia*, which he stated has shared a unique common ancestor with *Musa*, was placed in a separate subfamily. Obviously Lane accepted the phenetic view that the degree of char-acter differences, not the cladistic patterns, should determine the hierarchical level of classification.

Lane briefly mentioned that the cymose-type inflorescences of the other families of the Scitam-ineae indicate that they were not closely related to the Musaceae. The position of *Orchidantha* in the order was also unclear to him. Lane's brief treat-ment, although somewhat unusual in light of our current knowledge of the taxa, was the first to address concisely the evolutionary relationships of the genera of the Musaceae s.l. in terms of ances-tors and descendants.

Tomlinson's analysis. The exhaustive investiga-tions of the anatomy of the Zingiberales by Tom-linson in the 1950s and 1960s served as the im-petus for his pivotal paper on the phylogeny of the order (Tomlinson, 1962). Building on the work of earlier taxonomists, Tomlinson combined both mor-phological and anatomical characters into an anal-ysis of the evolutionary relationships of the eight families he recognized in the Scitamineae (Table 1). Based on the structure of the guard cells, pres-ence or absence of raphide sacs, and structure of the root stele, he suggested that the eight families could be separated into four "natural groups . . . according to greatest degree of affinity": Group 1
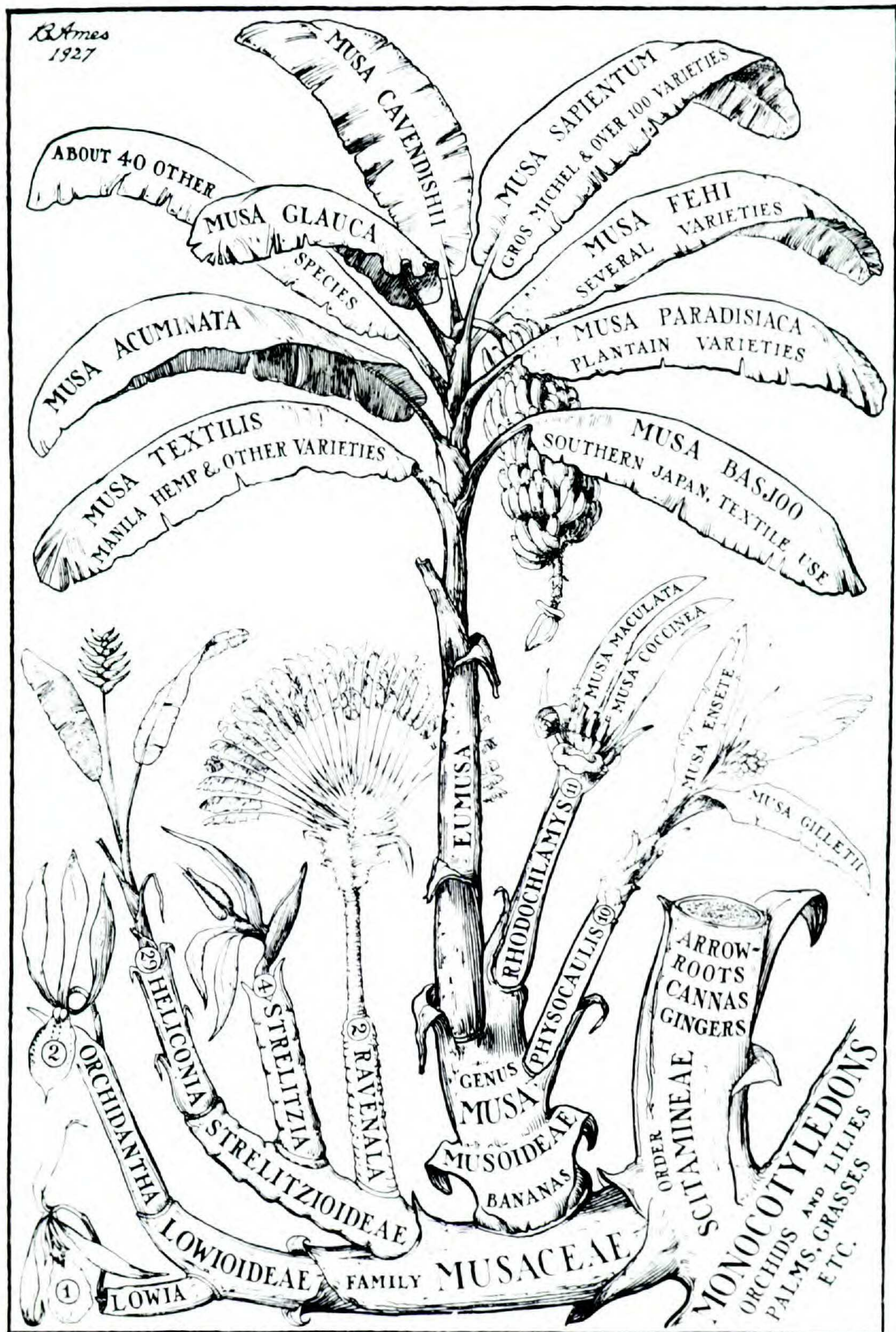
FIGURE 2. "Rhizogram" of the families of the Zingiberales. Rhizomatous patterns of growth are used to represent evolutionary branching relationships (from Reynolds, 1927).

(Heliconiaceae, Musaceae, and Strelitziaceae) with raphide sacs, symmetrical guard cells, and anomalous root structure (the last only in Musaceae and Strelitziaceae); Group 2 (Costaceae, Marantaceae, and Zingiberaceae) with asymmetrical guard cells, lack of raphide sacs, and normal root structure; Group 3 (Cannaceae) with symmetrical guard cells (variable), no raphide sacs, and normal root structure; and Group 4 (Lowiaceae) with raphide sacs,

asymmetrical guard cells, and normal root structure.

Tomlinson then went on to discuss evolutionary trends in floral and vegetative characters as a basis for understanding the historical relationships of the four groups in the order. He concluded that the ". . . Strelitziaceae was the most primitive family within the Scitamineae, in the sense that its members possess the greatest number of primitive floral

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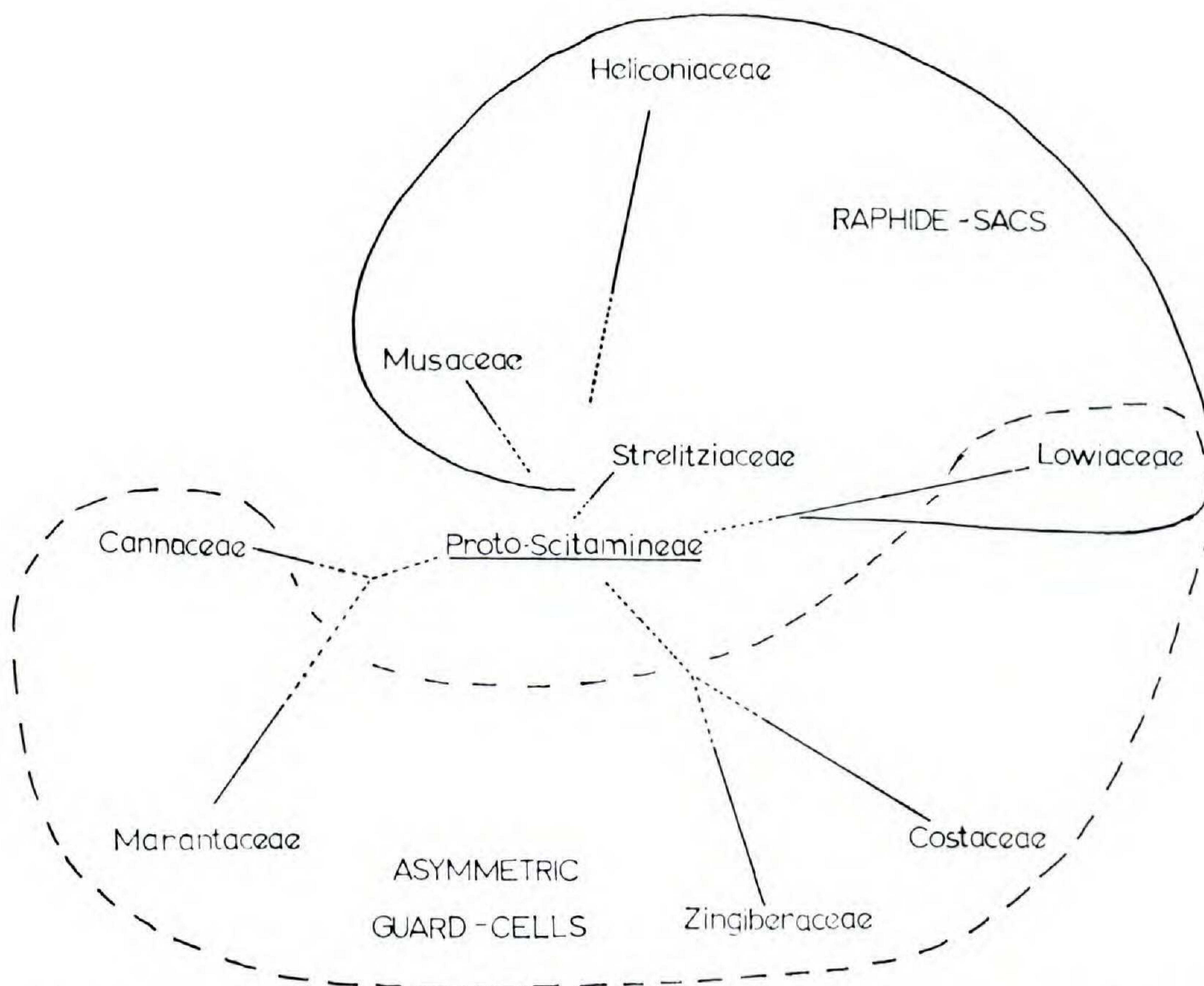of Zingiberales

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FIGURE 3. Tomlinson's two-dimensional concept of the evolutionary relationships of the eight families of the Zingiberales (from Tomlinson, 1962, his fig. 5).

features. Thus existing scitaminean flowers [and other vegetative and anatomical characters] can be regarded as derivative and advanced in varying degrees, compared with the strelitziaceous flower." Based on the assumption that the Strelitziaceae were the closest to a "proto-scitaminean" ancestor, Tomlinson diagrammatically represented the evolutionary relationships of the families (Fig. 3). However, the relationships depicted in his figure do not correspond to his four groups. In Group 1, the Heliconiaceae, Musaceae, and Strelitziaceae are positioned together in the figure, but each is on a separate line directly from the proto-scitaminean ancestor. Group 4, the Lowiaceae, is set in between Group 1 and the other families on its own distinctive line from the ancestor. Group 2 is divided into two separate lines. Two families of the group, Costaceae and Zingiberaceae, share a common branched line. The third family of Group 2, the Marantaceae, shares a common line with the only member of Group 3, the Cannaceae. The affinity of these last four families (plus the Lowiaceae) is depicted on the figure by a broken circle drawn around them, indicating the possession of asymmetrical guard cells (apparently erroneously including the Cannaceae). Likewise, the affinity of the families of Group 1 (plus Lowiaceae) is shown by a circle representing the presence of raphide sacs.

Tomlinson's publication on the Scitamineae, al-

though somewhat ambiguous in the correspondence between the classification and its diagrammatic representation, was the first phylogenetic analysis of the eight families of the order that was based on a methodical examination of character distribution. His use of a priori evolutionary "trends" in floral traits (e.g., the designation of the strelitziaceous flower as primitive) to develop concepts of primitive and advanced states of other features may be criticized as a questionable method of character polarization. In addition, the relationships of the Musaceae, Heliconiaceae, and Strelitziaceae were never fully resolved in his work. The analysis, however, provided a concise rationale for linking the Marantaceae to the Cannaceae and the Zingiberaceae to the Costaceae, as well as for the distinct position in the order of the Lowiaceae.

Bisson et al. (1968), as the result of a lengthy caryological analysis of the Zingiberales, supported Tomlinson's (1962) inferences on the evolutionary relationships of the eight families. They informally proposed three suborders: (1) Strelitziaceae, Musaceae, and Heliconiaceae; (2) Zingiberaceae and Cosaceae; and (3) Marantaceae and Cannaceae; excluding the Lowiaceae due to the lack of adequate cytological data.

Dahlgren & Rasmussen's analysis. The most recent analysis of the phylogenetic relationships of
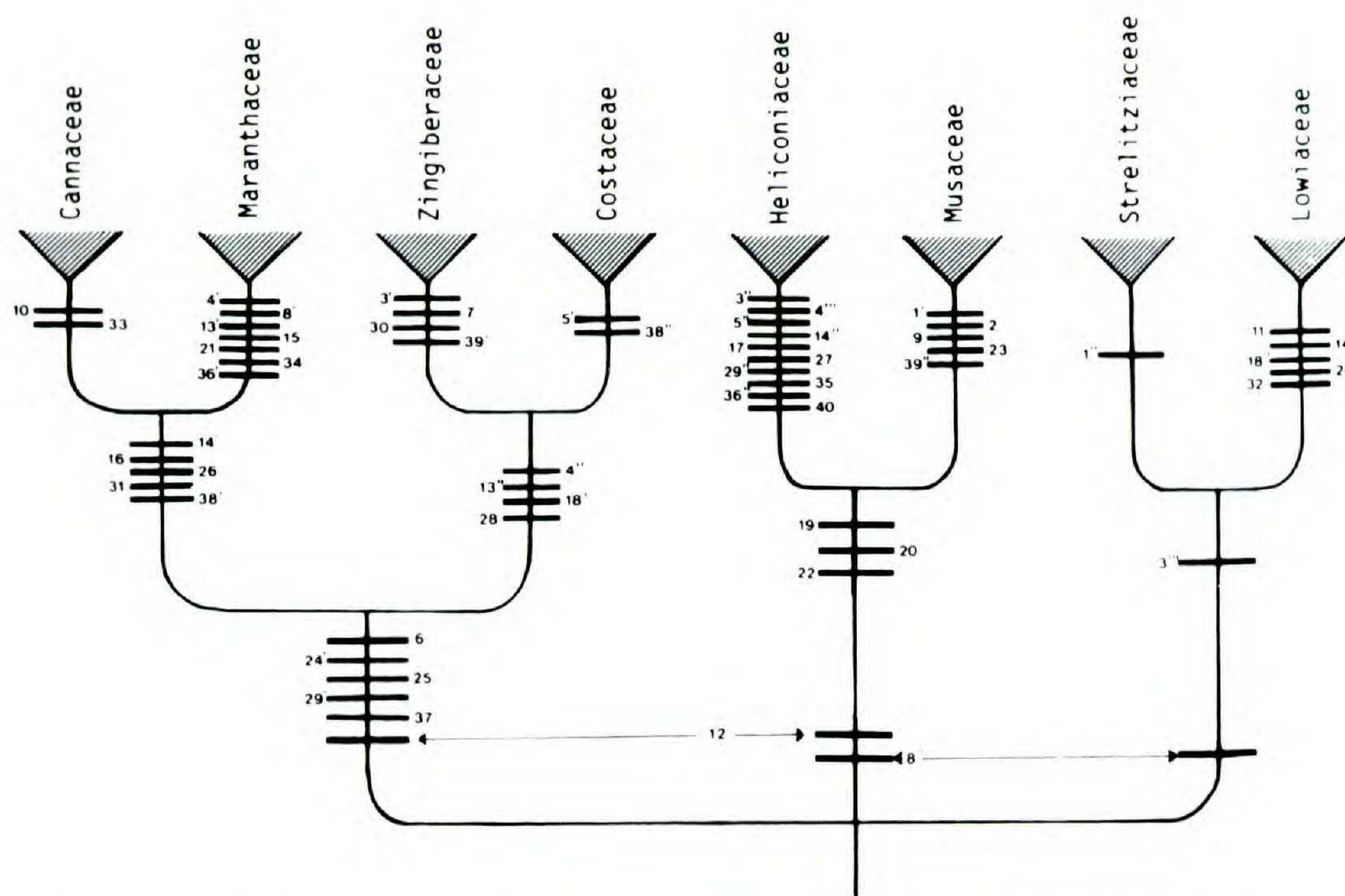
FIGURE 4. Cladogram of the Zingiberales resulting from the analysis of Dahlgren & Rasmussen (1983, their fig. 9).

the Zingiberales was by Dahlgren & Rasmussen (1983) in their publication on the evolution of the monocotyledons. They were not interested in the relationships of the order per se, but rather chose the group to demonstrate their method of cladistic analysis, which they advocated for an evaluation of the relationships of the monocotyledons as a whole. They selected the Zingiberales, accepting the eight families proposed by Nakai (1941), as an example "because of its unchallenged status as a monophyletic group . . . ."

Dahlgren & Rasmussen followed the basic procedures of Hennigian phylogenetic systematics by (1) selecting an outgroup, (2) polarizing characters of the ingroup based on the states present in the outgroup, and (3) grouping taxa according to shared derived character states (synapomorphies). They recognized that no unequivocal outgroup could be selected for the Zingiberales, but chose their Commeliniflorae (discussed earlier) as the best possible outgroup. The morphological and anatomical characters described by Tomlinson (1962, 1969) provided the basis for the 40 two-state character set for the analysis. Their cladogram was constructed by "hand" according to a method described in the paper.

The best-defined section of the resulting cladogram (Fig. 4) was the monophyletic "ginger group" (Zingiberaceae, Costaceae, Marantaceae, and Cannaceae) united by the lack of raphide sacs, single fertile stamen, and abundant perisperm. Two pairs of sister groups within the ginger group were also each defined by several apomorphies: the Costa-

ceae + Zingiberaceae by the fused staminodes; the Cannaceae + Marantaceae by the asymmetric flowers, bisporangiate anther, and specialized petaloid staminodes. Within the remaining four families of the order (the "banana group"), the Musaceae and Heliconiaceae were shown to be sister taxa based on the unique presence of the perianth tube, and the Strelitziaceae and Lowiaceae were united by their distichous phyllotaxy. However, due to the conflict presented by the distribution of two characters (terminal inflorescences and stegmata), some doubt was expressed as to whether the banana group formed a separate clade distinct from the ginger group. The thick-walled silica cells (stegmata) shared by the four banana families suggests that they are a monophyletic group. The presence of a terminal inflorescence in the Heliconiaceae, Musaceae, and the members of the ginger group unite those taxa. Dahlgren & Rasmussen considered the stegmata as the "more significant synapomorphy" and hence supported the monophyly of the banana group.

Dahlgren & Rasmussen's phylogeny of the Zingiberales does not conflict significantly with the scheme proposed by Tomlinson (1962). Both analyses accepted the two sister-group relationships within the ginger group (Marantaceae + Cannaceae; Costaceae + Zingiberaceae), and both considered the relationships of the four families of the banana group as somewhat unresolved. The monophyly of the four families of the ginger group is strongly supported by Dahlgren & Rasmussen. They also provided evidence for uniting as sister groups

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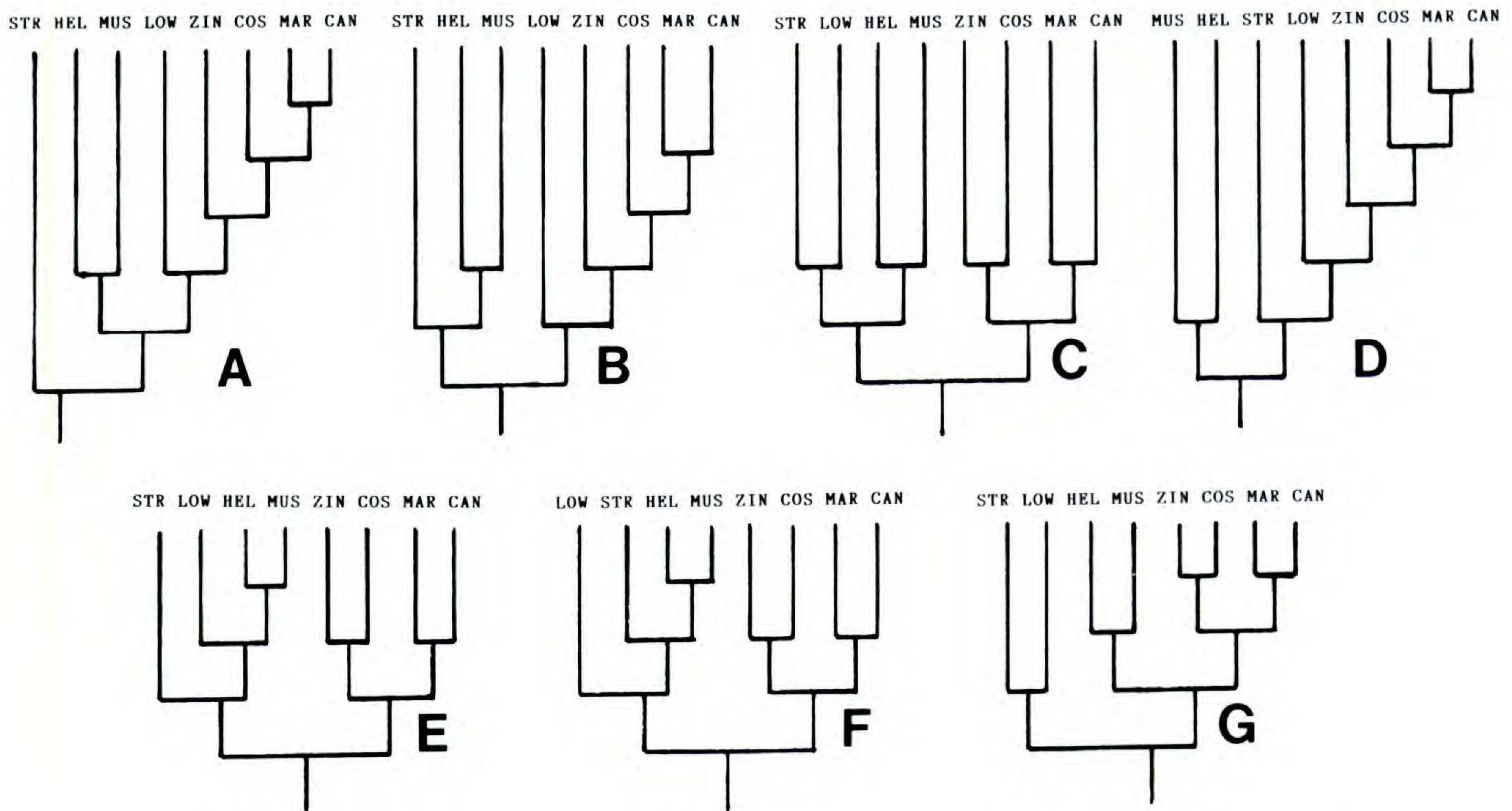of Zingiberales

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FIGURE 5. Seven equally parsimonious trees from Analysis One in which the character set of Dahlgren & Rasmussen (1983) was used.

the Heliconiaceae and Musaceae as well as the Lowiaceae and Strelitziaceae, but questioned the strength of this evidence. Their analysis is more explicit than Tomlinson's in its statements on the cladistic relationships of the families and the characters that define the monophyletic groups. Neither of the investigations suggested any new formal ranks.

Because of the formalized, explicit construction of the cladogram of Dahlgren & Rasmussen, it is possible to follow clearly their methods and provide a critique of the phylogeny. A close look at their data matrix reveals several problems, inconsistencies, and unnecessary characters in the analysis. Several of the 40 two-state characters used to construct the cladogram were coded incorrectly (e.g., characters 4 and 5: "uniseriate" is confused with "unicellular" trichomes; character 23: free median petal is found in the Musaceae and in the Strelitziaceae; character 30: all staminodes fused is an autapomorphy for the Costaceae, not the Zingiberaceae). Sixteen characters are coded (in some cases incorrectly) as being present in one family only, i.e., as autapomorphies for the terminal taxa, and therefore are of no value in determining relationships among the taxa (character 2: pseudobulbs; character 7: oil cells; character 9: articulated lacticifers; character 10: mucilage canals; character 11: axillary inflorescence; character 15: two-flowered inflorescences; character 17: resupinate flowers; character 21: corolla tube; character 23: free median petal; character 27: median

stamen of outer whorl missing; character 30: all staminodes fused; character 32: hypanthiumlike neck on ovary; character 33: petaloid style; character 34: less than three fertile locules per ovary; character 35: basal placentation; character 40: schizocarp). Of course autapomorphies are of critical importance in defining the monophylesis of the terminal taxa, but they provide no information on cladistic relationships. Another problem with the character analysis is the coding of characters that are variable or polymorphic within taxa (e.g., character 8: stegmata; characters 11, 12: inflorescence type; characters 24, 27: stamen number; character 34: number of locules per ovary). Polymorphic characters can be legitimately used in cladistic analysis if evidence is provided for designating which of the states is plesiomorphic in the taxon. Dahlgren & Rasmussen did not provide this information. Finally, misinterpretation of some character state homologies (especially in perianth features; see below) led to inaccurate coding in several taxa.

The most significant deficiency of the phylogeny is the lack of any demonstration that the arrangement of taxa and characters in the cladogram is the most logically acceptable or parsimonious one. No justification was provided as to why this cladogram is the best representation of the relationships of the taxa based on the distribution of the available characters. To test the hypothesis that the cladogram presented by Dahlgren & Rasmussen is the most parsimonious, the same 24 characters (the 16 autapomorphies listed above were omitted) with

no recording or changes in polarization were reanalyzed using a computer-assisted maximum parsimony method (D. Swofford's PAUP program; see below). This method for inferring phylogenies, which places no restrictions on character state changes and estimates minimum length trees, is based on the same principles as the method used by Dahlgren & Rasmussen. Seven equally parsimonious cladograms (each with the same number of character state changes) were found (Fig. 5). The topology of each of the seven cladograms, which included the arrangement(s) presented by Dahlgren & Rasmussen (Fig. 5C, G), differed significantly in the relationships of the eight families. The sister-group relationships of the Heliconiaceae + Musaceae and the Marantaceae + Cannaceae were the only two consistencies in all seven of the cladograms. These results indicate that the analysis by Dahlgren & Rasmussen was not only incomplete, but that the character set they used is not sufficient (with the included inaccuracies) to determine unambiguously the phylogenetic relationships of the families of the Zingiberales.

THE PHYLOGENY OF THE ZINGIBERALES

The phylogenetic analysis performed by Dahlgren & Rasmussen (1983) was the first attempt to infer historical relationships of the eight families of the Zingiberales using the methods of phylogenetic systematics. However, as pointed out above, their results are suspect due to certain flaws in the analysis. Nevertheless, their cladistic methods were sound, and sufficient documentation was provided to repeat the analysis and test their hypothesis of the phylogeny of the Zingiberales.

An independent, original analysis of the Zingiberales using cladistic methods was initiated in the present investigation to clarify the conflicts, inconsistencies, and omissions of previous investigations. The aim of the study was to devise an unambiguous character set that would allow the estimation of a fully resolved cladogram to serve as the basis for a new hierarchical classification reflecting phylogenetic relationships.

MATERIALS AND METHODS

The eight families of the Zingiberales proposed by Nakai (1941) and accepted by Tomlinson (1962, 1969), Cronquist (1978, 1981), Dahlgren & Rasmussen (1983), and Dahlgren et al. (1985) were used as the operational taxonomic units in the present analysis. The autapomorphies listed earlier in the individual family descriptions are accepted as evidence for the monophyly of each of the families.

The characters used for inferring relationships were taken from a number of sources, including my own published and unpublished investigations. Lane (1955), Tomlinson (1956, 1959, 1961, 1962, 1969), and Dahlgren et al. (1985) were consulted for basic morphological and anatomical characters. Conflicts in the distribution of character states among these references were resolved by original observations where possible or by further reference to the works of other workers on specific families or characters, e.g., Humphrey (1896), Gatin (1908), Cheesman (1947), Holttum (1950, 1970), Simmonds (1962), Larsen (1966), Bisson et al. (1968), Mahanty (1970), Burtt (1972), Maas (1972, 1977), Wagner (1977), Williams & Harborne (1977), Goldblatt (1980), Olatunji (1980), Andersson (1981), Barthlott & Frölich (1983), Kirchoff (1983a, b, 1986), Kress (1984), and Rogers (1984).

In the Zingiberales, as is true in most plant groups, many characters are variable within the family. Unless the primitive state of a polymorphic character is known a priori, that character cannot be unequivocally coded and used in the analysis (Mickevich & Mitter, 1981). For this reason some variable characters were omitted from the analysis, e.g., cytology, stomatal type, septal nectaries, endosperm type, embryo shape, fruit type. Additional characters that may provide evidence on relationships, such as leaf flavonoids, are not known for all families (and are often variable in those taxa in which they are known) and were not included in the analysis in most cases. After attempting to assign states to more than 50 characters of the eight families, 32 characters (primarily floral morphology and vegetative anatomy) initially appeared unambiguous or "solid" enough to incorporate into the analysis (Table 2). All characters were defined to have two states to avoid the problems of devising a transformation series for multistate characters. Autapomorphies of the families, listed earlier in the family descriptions, were not included in the analysis.

Pollen characters were specifically omitted from the analysis even though a considerable amount is now known about the pollen of various families (e.g., Muller-Stoll, 1956; Saad & Ibrahim, 1965; Erdtman, 1966; Punt, 1968; Skvarla & Rowley, 1970; Kress et al., 1978; Stone et al., 1979, 1981; Kress & Stone, 1982, 1983; Hesse & Waha, 1983; Kress, 1986; Stone & Kress, unpublished). This information was not included because the cladogram resulting from the present analysis will

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TABLE 2. Characters used in Phylogenetic Analyses Two and Three.

Character	Character states
1. Anticlinal walls of leaf epidermal cells	sinuous (0)[1] not sinuous (1)
2. Leaf guard cells	symmetrical (0)[1] asymmetrical (1)
3. Leaf adaxial hypodermis	≥1 cell layer (0)[1] 1 cell layer (1)
+4. Leaf longitudinal veins	independent of leaf surface (0)[1] attached to leaf surface (1)
+5. Leaf transverse veins	sheathed (0)[1] not sheathed (1)
+6. Transverse vein sheathing cells	thick-walled (0)[1] thin-walled (1)
7. Air canals in leaf axis	1 arc (0)[1] 2 arcs (1)
8. Root stele	polyarc (0)[1] with medullary vessels & phloem (1)
9. Raphide sacs	present (0)[1] absent (1)
10. Internal silica cell bodies — hat-shaped	absent (0)[1] present (1)
11. Internal silica cell bodies — trough-shaped	absent (0)[1] present (1)
12. Internal silica cell bodies — druse-shaped	absent (0)[1] present (1)
+13. Superficial cells with silica bodies	present (0)[1] absent (1)
14. Vessels	roots & stems (0)[1] roots only (1)
15. Phyllotaxy	spirally arranged (0)[1] distichous (1)
16. Flower shape	zygomorphic (0)[1] asymmetric (1)
+17. Sepals and petals fused into tube	no (0)[1] yes (1)
++18. All sepals	not fused (0)[1] fused at least at base (1)
++19. All petals	not fused (0)[1] fused at least at base (1)
+++20. Median petal	free (0)[1] fused to lateral petals (1)
21. Fertile stamen number	≥5 (0)[1] 1 (1)
22. Inner whorl median stamen	present/fertile (0)[1] absent (1)
23. Outer whorl median stamen	fertile (0)[1] not fertile (1)

TABLE 2. Continued.

Character	Character states
24. Outer whorl median stamen	present (0)[1] absent (1)
25. Outer whorl lateral stamens	fertile (0)[1] staminodia (1)
26. Inner whorl lateral stamens	fertile (0)[1] staminodia (1)
27. Staminodes	not fused (0)[1] variously fused for most of length (1)
28. Anther(s)	tetrasporangiate (0)[1] bisporangiate (1)
29. Style	unmodified (0)[1] modified (1)
30. Ovule placentation	axile (0)[1] basal (1)
31. Aril	absent (0)[1] present (1)
+++32. Well-developed perisperm	absent (0)[1] present (1)
33. Endosperm	helobial (0)[1] nuclear (1)
34. Chalazosperm	absent (0)[1] present (1)

[1] Character state present in outgroup (Bromeliiflorae) and coded as primitive in the Zingiberales.
+ Omitted in Analysis Three.
++ Recoded in Analysis Three.
+++ Added to Analysis Three.

be used to infer the evolution of pollen wall structure in the Zingiberales in subsequent investigations (Kress & Stone, unpublished; see below).

The Bromeliiflorae of Dahlgren et al. (1985) was selected as the outgroup of the Zingiberales and the characters were polarized accordingly. The state common to the two groups was coded as the primitive state. For characters variable in the Bromeliiflorae (15, 17, 21), the state present in the Bromeliales (Bromeliaceae) was chosen as the primitive state in that superorder. In several cases, character states were unknown or nonexistent for some taxa and were coded as "missing."

The computer program PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 1985) was used to infer the most parsimonious phylogeny. The "branch and bound" option (BANDB) of PAUP, which guarantees that the shortest trees will be found (if fewer than ten taxa), was used in conjunction with the ancestor rooting option (ROOT

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TABLE 3. Taxon by character matrix for the eight families of the Zingiberales and 34 characters used in Phylogenetic Analyses Two and Three.

Family	Character																		
	1	2	3	4¹	5¹	6¹	7	8	9	10	11	12	12²	13¹	14	14²	15	16	17¹
Lowiaceae	1	1	1	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0
Musaceae	1	0	0	1	1	9	0	1	0	0	1	0	0	1	1	1	0	0	1
Heliconiaceae	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	1
Strelitziaceae	9	0	0	1	1	9	1	1	0	0	0	1	1	0	0	0	1	0	0
Zingiberaceae	1	1	1	1	0	1	0	0	1	0	0	9	0	0	1	0	1	0	0
Costaceae	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Cannaceae	1	0	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
Marantaceae	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	1	1	0

0 = Primitive state.
1 = Advanced state.
9 = Missing character.
¹ = Omitted in Analysis Three.
² = Recoded in Analysis Three.
³ = Added to Analysis Three.

= ANCESTOR) and the Farris method of HTU character state optimization (OPT = FARRIS).

Three separate analyses were run. The first was a test of the parsimony of the phylogeny derived by Dahlgren & Rasmussen (1983) and used the same characters (24, excluding the 16 autapomorphies) and polarity coding. The second and third analyses incorporated 34 independently derived characters (autapomorphies also excluded; Tables 2 and 3) and used the Bromeliiflorae as the outgroup.

After construction of the cladogram from the first independent character set (Analysis Two), character evolution was traced on the cladogram. As a result of the patterns revealed by the cladogram, each character was then reevaluated for defendable hypotheses of homology and accurate coding. Five characters (4: longitudinal veins; 5: leaf transverse veins; 6: transverse vein sheathing; 13: superficial cells with silica bodies; 17: sepal and petal fusion) could not be unambiguously coded because of variability in the outgroup, variability within families of the ingroup, or initial inaccurate morphological examination, and were omitted. Five characters (12: druse-shaped silica bodies; 14: vessels; 18: fusion of the sepals; 19: fusion of the petals; 23: outer whorl medium stamen) required recoding because of original mistakes in coding due to faulty literature reports. Two new informative characters (20: fusion of median petal; 33: perisperm) that were not included in the first original analysis were found. As a result of this character reevaluation, a second analysis (Analysis Three) was performed using the same PAUP options and a revised data set with characters omitted, recoded,

or added as just described (29 total characters; Tables 2 and 3).

RESULTS

Analysis One: reevaluation of Dahlgren & Rasmussen study. The reanalysis of the character set of Dahlgren & Rasmussen, as discussed above, yielded seven equally parsimonious trees (Fig. 5), each with a total of 41 evolutionary steps (including 17 homoplasies; Consistency Index = 0.585). The seven trees included the two cladograms (Fig. 5C, G) of their analysis.

Analysis Two. The first of the independent analyses using the original set of 32 characters polarized with the Bromeliiflorae produced three equally parsimonious trees (Fig. 6A–C), each with 63 character state changes, including 31 homoplasies (Consistency Index = 0.508; F-value = 6.164–6.480). Each of these cladograms is fully resolved with all branching points dichotomous. The largest clade consistent in all three trees includes the Lowiaceae, Costaceae, Zingiberaceae, Cannaceae, and Marantaceae with the same sister group relationships in each tree. Autapomorphies of the Marantaceae–Cannaceae clade are asymmetric flowers (character 16), unfused staminodes (character 27), bisporangiate anthers (character 28), and a modified style (character 29). This clade is united with the Zingiberaceae by the absence of the median stamen in the outer staminal whorl (character 24). Synapomorphies of the clade formed by the Costaceae and Zingiberaceae–Cannaceae–Marantaceae are the absence of raphide sacs (character

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TABLE 3. Continued.

										Character									
18	18²	19	19²	20³	21	22	23	23²	24	25	26	27	28	29	30	31	32³	33	34
1	1	0	0	0	0	1	0	0	0	0	0	9	0	0	0	1	0	9	0
0	1	1	0	0	0	1	0	0	0	0	0	9	0	0	0	0	0	1	0
0	0	1	1	1	0	0	1	1	0	0	0	9	0	0	1	0	0	1	0
0	0	0	0	0	0	1	0	0	0	0	0	9	0	0	0	1	0	1	0
1	1	0	1	1	1	0	1	9	1	1	1	1	0	0	0	1	1	0	0
1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1
0	0	1	1	1	1	0	1	9	1	1	1	0	1	1	0	0	1	1	1
0	0	1	1	1	1	0	1	9	1	1	1	0	1	1	1	1	1	1	1

9), presence of a single fertile stamen (character 21), and staminodia in the lateral positions of the inner and outer staminal whorls (characters 25, 26). The Lowiaceae are united to this four-family clade by the asymmetric guard cells (character 2; lost in the Cannaceae) and the fused sepals (character 18; not shared by the Cannaceae–Marantaceae clade; this character was recorded for Analysis Three).

The variable lineages of the three equally parsimonious trees in Analysis Two are due to the unstable positions of the Musaceae, Heliconiaceae, and Strelitziaceae. In the first tree (Fig. 6A), the Musaceae and Heliconiaceae are sister groups united by the trough-shaped internal silica cell bodies (character 11) and the fused sepals and petals (character 17; this misinterpreted character is omitted in Analysis Three), as well as several other homoplasious characters (character 6: transverse vein sheathing cells; character 19: petals; character 31: no aril). In the other two trees (Fig. 6B, C) the Musaceae and the Strelitziaceae form a monophyletic lineage based on the shared unsheathed transverse leaf veins (character 5; variable and omitted in Analysis Three), the root stele with medullary vessels and phloem (character 8), and three homoplasious characters (character 3: multilayered leaf adaxial hypodermis; character 4: attached leaf longitudinal veins; character 22: inner whorl median stamen absent). No uniquely derived characters unite any of these lineages to the Lowiaceae–Costaceae–Zingiberaceae–Cannaceae–Marantaceae group in the three trees.

In all three of the trees, four characters change states between the outgroup (the Bromeliiflorae) and the common ancestor of the Zingiberales, and hence are additional synapomorphies of the order: two arcs of air canals in the leaf axis (character 7), distichous phyllotaxy (character 15), staminodia fused (character 27; not applicable to four of the

eight families that possess one or no staminodium), and nuclear endosperm (character 33).

Among the three trees there are 11 uniquely derived character states, mostly floral traits, nine of which are common to all trees (character 9: raphide sacs absent; character 16: asymmetric flowers; character 21: one fertile stamen; character 24: outer whorl median stamen absent; character 25: outer whorl lateral stamens sterile; character 26: inner whorl lateral stamens sterile; character 27: staminodes not fused; character 28: bisporangiate anthers; character 29: modified style).

Analysis Three. In the reanalysis of the original 32 characters in which characters were omitted (characters 4, 5, 6, 13, 17), recoded (characters 12, 14, 18, 19, 23), or added (characters 20, 32), a single shortest tree (Fig. 7) was found with a total length of 53 steps, including 24 homoplasies (Consistency Index = 0.547; F-value = 4.939). Fifteen characters are uniquely derived (character 8: poly-arc root stele; character 9: raphide sacs absent; character 16: asymmetric flowers; character 19: petals fused at base; character 20: median petal fused to lateral petal; character 21: one fertile stamen; character 22: inner whorl median stamen present; character 23: outer whorl median stamen not fertile; character 25: outer whorl lateral stamens sterile; character 26: inner whorl lateral stamens sterile; character 27: staminodes fused; character 28: anther bisporangiate; character 29: style modified; character 32: well-developed perisperm; character 33: helobial endosperm). The cladogram is fully resolved with all branching points dichotomous. The Cannaceae and Marantaceae form a terminal monophyletic lineage defined by asymmetric flowers (character 16), bisporangiate anthers (character 28), and a modified style (character 29). The Zingiberaceae and Costaceae, a second terminal group, are united by the uniquely
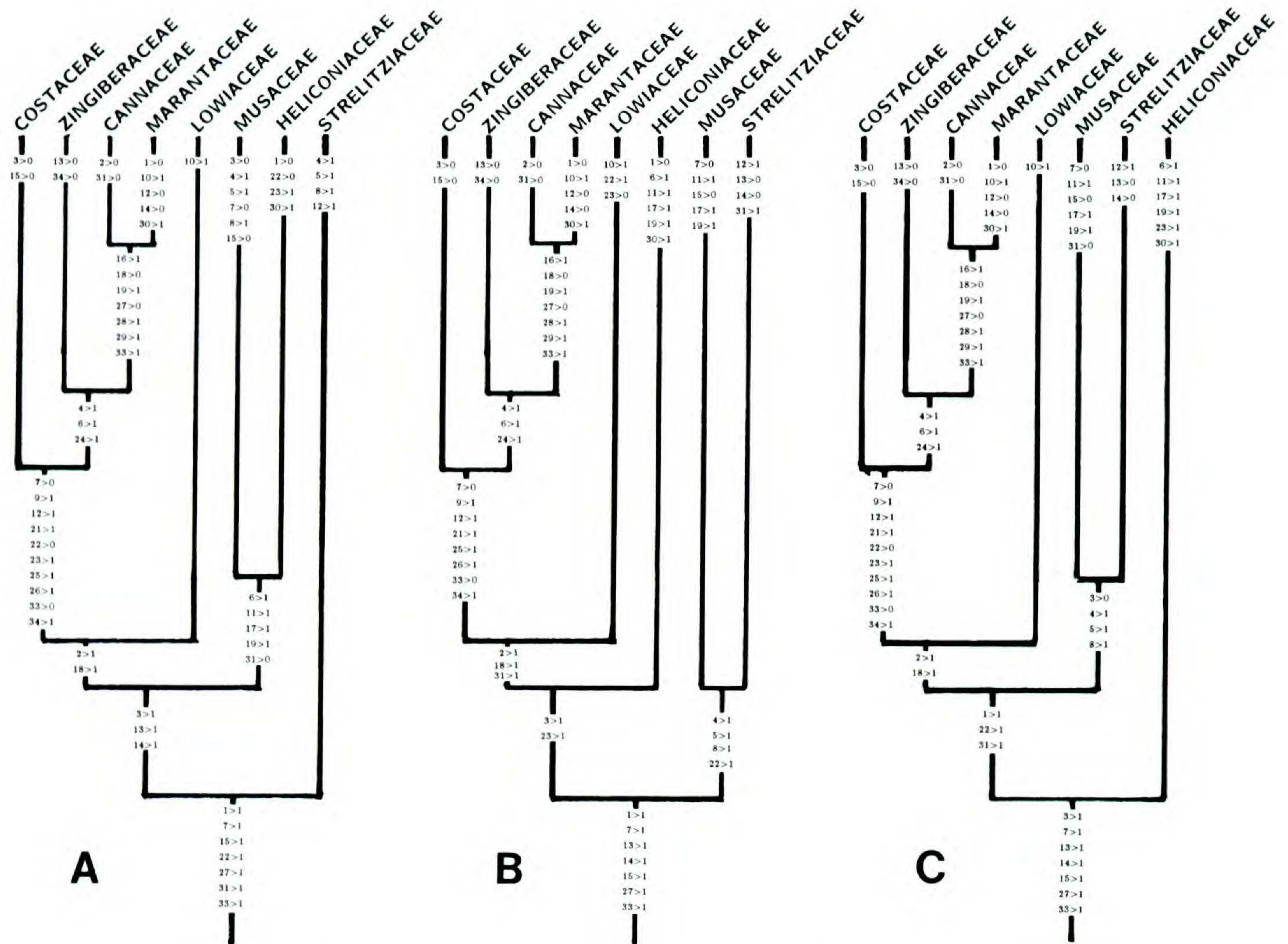
FIGURE 6. Three equally parsimonious cladograms of the Zingiberales resulting from Analysis Two. Numbers to the left of the arrows (>) refer to characters listed in Tables 2 and 3; numbers to the right of the arrows are apomorphic character states at that node.

derived fused staminodes (character 27) and helobial endosperm (character 33) as well as the homoplasious fused sepals (character 18; also in the Lowiaceae). Synapomorphies of the clade made up of these four families are the loss of raphide sacs (character 9), reduction in fertile stamens to one (character 21), staminodia in the lateral positions of the inner and outer whorls of stamens (characters 25, 26), and the well-developed perisperm (character 32). The single arc of air canals in the leaf axis (character 7; also in Musaceae), absence of the median stamen in the outer staminal whorl (character 24; regained in Costaceae), and the presence of chalazosperm (character 34; lost in Zingiberaceae) are homoplasies that also unite these families.

The Heliconiaceae are the sister group of the four-family "ginger group," sharing the basally fused petals (character 19), the median petal fused to the lateral petals (character 20), the presence of the median stamen of the inner staminal whorl (character 22), and the infertile stamen (i.e., staminode) in the median position of the outer staminal whorl (character 23), all of which are uniquely

derived states on the tree. The Lowiaceae are joined to this five-family clade on the basis of the shared polyarc root stele (character 8), asymmetrical guard cells (character 2; symmetrical in the Cannaceae), and the one cell-layered leaf hypodermous (character 3; multiple layers in the Costaceae).

The sister taxon of the lineage formed by the Lowiaceae–Heliconiaceae–Costaceae–Zingiberaceae–Cannaceae–Marantaceae is the Strelitziaceae. Three homoplasious character states unite them: two arcs of air canals in the leaf axis (character 7; reversed to one arc in the ginger group), distichous phyllotaxy (character 15; reversed in the Costaceae), and the arillate seeds (character 31; lost in the Heliconiaceae and Cannaceae). These seven families share a common ancestor with the Musaceae, the eighth family of the order.

Five character states derived in the common ancestor are homoplasious in the order: nonsinuous anticlinal walls of the leaf epidermal cells (character 1; independently becoming sinuous in Heliconiaceae and Marantaceae), root stele with medullary vessels and phloem (character 8; polyarc in the Lowiaceae–Heliconiaceae–ginger group), vessels

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restricted to the roots (character 14; vessels independently reappearing also in stems in the Strelitziaceae, Zingiberaceae, and Marantaceae), absence of the median stamen of the inner staminal whorl (character 22; regained in the Heliconiaceae–ginger group), and nuclear endosperm (character 33; helobial in Zingiberaceae–Costaceae).

DISCUSSION

Character analysis. Continual reassessment and reexamination of character state identification, distribution, and homology is the basis of any phylogenetic analysis. In the present investigation of the Zingiberales, the problem posed by the seven conflicting but equally parsimonious trees (Fig. 5) derived from the Dahlgren & Rasmussen character set was partly resolved by the reevaluation of their data. The three cladograms subsequently constructed in Analysis Two (Fig. 6) forced a further evaluation and reanalysis of the original characters leading to the single shortest tree produced in Analysis Three (Fig. 7).

Floral characters have presented much difficulty in assigning probable homologous states. For example, Dahlgren & Rasmussen (1983) mistakenly interpreted all three perianth characters that they used to unite the Musaceae and Heliconiaceae (their character 19: all sepals fused with petals into a tube; character 20: some sepals not part of perianth tube; character 22: petals part of a perianth tube). Although there is a "perianth tube" in both families, in the Musaceae it is made up of three fused sepals and two fused petals (the median petal free), while in the Heliconiaceae it is formed by two fused sepals and three fused petals (the median sepal is free). These "tubes" are certainly not homologous structures, and hence cannot unite the two families. In none of the families of the Zingiberales are "all sepals fused with [all] petals into a perianth tube" as they have defined their character number 19. The "corolla tube" (their character 21), assigned by Dahlgren & Rasmussen only to the Marantaceae, is also present in the Zingiberaceae, Costaceae, Cannaceae, and Heliconiaceae and is a synapomorphy of those five families according to Analysis Three.

The position in the two staminal whorls of the modified or missing stamens is also an important character that must be coded carefully. In the independent analyses conducted here, each position was designated as a separate character in assigning homologies. The sterile or lost stamen in the median position of the outer staminal whorl (characters 23, 24) and the fertile stamen in the
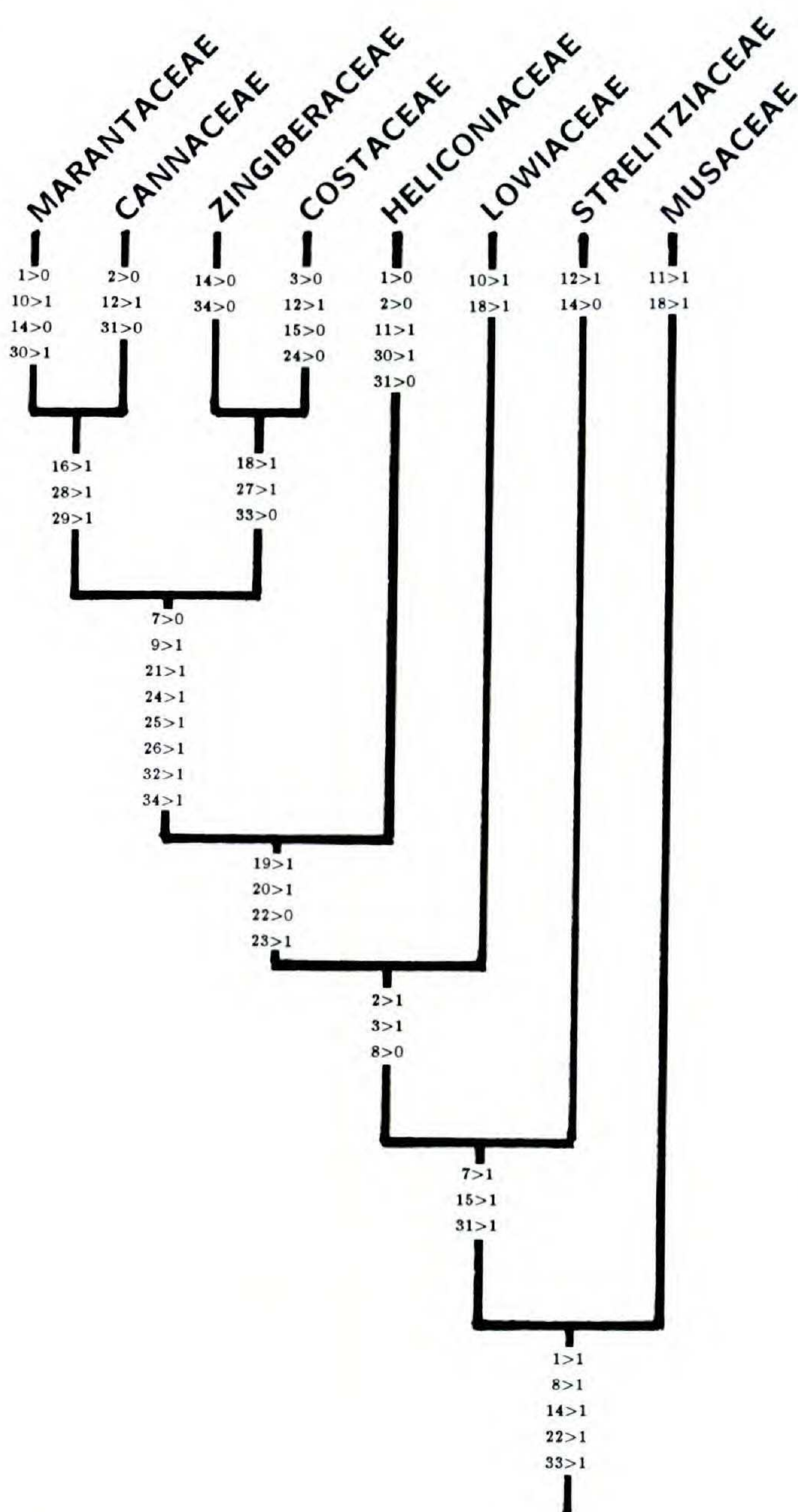

FIGURE 7. Most parsimonious cladogram of the Zingiberales resulting from Analysis Three. Numbers to the left of the arrows (>) refer to characters listed in Tables 2 and 3; numbers to the right of the arrows are apomorphic character states at that node.

median position of the inner staminal whorl (character 22) are thus interpreted as synapomorphies of the Heliconiaceae, Zingiberaceae, Costaceae, Cannaceae, and Marantaceae. The progressive evolutionary modification of the stamens into staminodes can be interpreted as beginning with the alteration of the outer median stamen in the Heliconiaceae followed by the outer and inner lateral stamens in the common ancestor of the other four families (the ginger group). The loss of the inner median stamen in the Musaceae, Strelitziaceae, and Lowiaceae is thus either an apomorphic loss in the common ancestor of the order that was regained in the common ancestor of the Heliconiaceae + ginger group, or three independent losses in those three families. The fact that at least one member

TABLE 4. Linnaean classification of the Zingiberales based on the cladistic relationships expressed in Figure 7 using the sequencing convention of Nelson (1972, 1974) and Wiley (1981).

Superorder Zingiberiflorae Dahlgren, Clifford & Yeo
  Order Zingiberales Nakai
    Suborder Musineae Kress, subord. nov.
      Family Musaceae A. L. Jussieu
    Suborder Strelitzineae Kress, subord. nov.
      Family Strelitziaceae Hutchinson
    Suborder Lowineae Kress, subord. nov.
      Family Lowiaceae Ridley
    Suborder Heliconineae Kress, subord. nov.
      Family Heliconiaceae Nakai
    Suborder Zingiberineae Kress, subord. nov.
      Superfamily Zingiberariae Kress, superfam. nov.
        Family Zingiberaceae Lindley
        Family Costaceae Nakai
      Superfamily Cannariae Kress, superfam. nov.
        Family Cannaceae A. L. Jussieu
        Family Marantaceae Petersen

of the Strelitziaceae (*Ravenala*) and possibly the Musaceae (*Ensete*; Dahlgren et al., 1985) possess this sixth stamen supports the second hypothesis and suggests the necessity of recoding character 21 (number of fertile stamens) in these two families.

In the Costaceae and the Zingiberaceae the staminodes are variously fused to each other (character 27), which was interpreted here as a synapomorphy of the two families. However, on closer inspection this fusion may not be homologous: all five staminodes are fused to form the labellum in the Costaceae, while only the two inner staminodes are united in the Zingiberaceae. Furthermore, several members of the Cannaceae show partial fusion of the staminodes, which in some cases can be fused basally to the corolla tube. If this character is homologous in these three families, then it is plesiomorphic in the ginger group (subsequently lost in the Marantaceae) and not a synapomorphy of the Costaceae–Zingiberaceae.

In the Marantaceae and the Cannaceae, the number of staminodes (three or four) varies among taxa. The presence of four staminodes was chosen as the state found in the common ancestor of these families (Fig. 1), which implies an independent loss of a staminode in each lineage. Additional investigations of the distribution and ontogeny of the various staminodes in the families of the ginger group are needed (e.g., Kirchoff, 1983a, b, 1986).

Only two of the 14 vegetative characters used in the third analysis are uniquely derived. The polyarc root stele (character 8) is interpreted as a synapomorphy of the Lowiaceae–Heliconiaceae–ginger group lineage, even though a similar feature is found in the outgroup. The absence of raphide sacs (character 9) evolved in the common ancestor of the ginger group and unites those four families. These two characters also furnished critical evidence for Tomlinson's (1962) recognition of natural groups in the Zingiberales. His third character, guard cells (character 2), is not uniquely derived in the present interpretation of the relationships.

Monophyletic groups. The results of the present analyses differ from previous classifications primarily in the recognition of the paraphyly of the group of "banana families" (Musaceae, Strelitziaceae, Heliconiaceae, and Lowiaceae). Earlier investigators (e.g., Bentham & Hooker, 1883; Schumann in Engler, 1900; Winkler in Engler & Prantl, 1930b; Lane, 1955; Tomlinson, 1962) united the genera of the banana group on the basis of the shared symmetrical guard cells, raphide sacs, and/or stamen number (five or six), all of which have been interpreted here as primitive (plesiomorphic) characters present in the common ancestor of the order. The inclusion of the members of these four families (or excluding Lowiaceae: Lane, 1955; Tomlinson, 1962) into the single family Musaceae s.l. has no cladistic basis.

The position of the Lowiaceae has always been controversial. Many unique floral and vegetative characters isolate this family from the other families of the order. In this analysis only the polyarc root stele provides evidence for its cladistic relationship to the Heliconiaceae and the ginger group.

The distichous phyllotaxy and the arillate seeds are the main features that unite the Strelitziaceae with the other six families of the order and exclude the Musaceae as the most "primitive" taxon. In this analysis the arborescent nature of the Strelitziaceae is a derived character and not a primitive feature as Tomlinson (1962) suggested.

The position of the Heliconiaceae as sister group to the four ginger families has not been acknowledged by any previous worker. The four floral synapomorphies shared by the Heliconiaceae and the ginger group provide evidence for uniting these families. The bananalike vegetative characters of *Heliconia* are plesiomorphies shared with the Musaceae and Strelitziaceae that have until now tended to obscure placement of this genus in the order.

The close relationship of the four families of the ginger group (Zingiberaceae, Costaceae, Cannaceae, and Marantaceae) has always been recognized (e.g., Tomlinson, 1962; Dahlgren et al., 1985), and the monophyly of this family group is supported

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TABLE 5. Phylogenetic key to the order Zingiberales based on Figure 7.

1a. Lacticifers present; flowers unisexual, plants monoecious. (*Cellulae lactiferae praesentes; flores unisexuales, plantae monociae.*) .... Suborder Musineae (Musaceae)
1b. Lacticifers absent; flowers bisexual 2
    2a. Root stele with medullary vessels and phloem; stem woody; two lateral petals fused to enclose anthers. (*Radicis stela vasibus medullosis et phloemate instructa; caulis lignosus; petala duo lateralia connata, antheras includentia.*) .... Suborder Strelitzineae (Strelitziaceae)
    2b. Root stele polyarc; stem not woody; two lateral petals not so fused 3
        3a. Sepals fused to form a solid tube; petals not fused; median petal free, forming labellum; median stamen of outer whorl fertile; median stamen of inner whorl absent. (*Sepala connata, tubum solidum formantia; petala non connata; petalum medianum liberum, labellum formans; stamen medianum verticilli exterioris fertile, interioris absens.*) .... Suborder Lowineae (Lowiaceae)
        3b. Sepals not forming a solid tube; petals fused at least at base; median petal not forming labellum; median stamen of outer whorl modified, sterile; median stamen of inner whorl present 4
            4a. Two arcs of air canals in leaf axis; raphide sacs present; fertile stamens 5; lateral stamens of inner and outer whorls fertile; perisperm absent (*Arcus duo canalium aeriorum in axe folii siti; saci raphidibus instructi praesentes; stamina quinque fertilia, lateralia verticillorum interiorum exteriorumque fertilia; perispermium absens.*) ....
.... Suborder Heliconineae (Heliconiaceae)
            4b. One arc of air canals in leaf axis; raphid sacs absent; fertile stamen 1; lateral stamens of inner and outer whorls sterile; perisperm present. (*Arcus unus canalium aeriorum in axe folii situs; saci raphidibus instructi absentes; stamen singulum fertile; stamina lateralia verticillorum interiorum exteriorumque sterilia; perispermium praesens.*) ....
.... 5. Suborder Zingiberineae
        5a. Flowers zygomorphic; sepals fused at base; style unmodified, situated between anther sacs; anther tetrasporangiate; endosperm helobial. (*Flores zygomorphi; sepala in base connata; stylus immutatus, inter sacos antherarum situs; anthera tetrasporangifera; endospermium instar Helobiarum.*) .... Superfamily Zingiberariae
            6a. Phyllotaxy distichous; aromatic oils present in vegetative body; inner lateral staminodes fused into a labellum .... Zingiberaceae
            6b. Phyllotaxy spirally arranged; aromatic oils not present in vegetative body; all staminodes fused into a labellum .... Costaceae
        5b. Flowers asymmetric; sepals free; style modified, separated from anther; anther bisporangiate; endosperm nuclear. (*Flores asymmetrici; sepala libra; stylus mutatus, ex anthera discretus; anthera bisporangifera; endospermium non cellulosum.*) ....
.... 7. Superfamily Cannariae
            7a. Mucilage cells absent from stems; pulvinus present; sigmoid lateral veins with evenly spaced cross veins in leaves; terminal pairs of enantiomorphic flowers; inner stamens modified into cucullate and callous staminodes; style not petaloid; single ovule per locule .... Marantaceae
            7b. Mucilage cells in stems; pulvinus absent; lateral veins oblique in leaves; petaloid style; flower pairs not enantiomorphic; inner staminodes and style petaloid; multiple ovules per locule .... Cannaceae

by a large suite of synapomorphies. The controversy over the recognition of the Costaceae as a separate family from the Zingiberaceae is not resolved except to show that these two families form a distinct monophyletic lineage not cladistically inconsistent with the recognition of a single family Zingiberaceae.

The cladograms presented here and the work by Dahlgren & Rasmussen (1983) provide the only explicit, fully resolved representations of the phylogenetic relationships of the Zingiberales. The consistencies and inconsistencies among these trees are an indication of the problems and complexities of character analysis and the resultant interpretation of sister-group relationships among the families. The only consistent lineages in all trees are

the four families of the ginger group and the Cannaceae–Marantaceae.

A new classification of the Zingiberales. One of the goals of this investigation was to derive a new classification of the order that reflected cladistic relationships. A strict cladistic hierarchical classification based on Figure 7 would be very complex. Because of the paraphyletic nature of the banana families, five ranks would be required between the order and family levels, four of which would include only a single family. For this reason a modified classification based on the cladistic relationships but following the "sequencing convention" of Nelson (1972, 1974) and Wiley (1981) is suggested (Table 4). The sequencing convention allows mono-
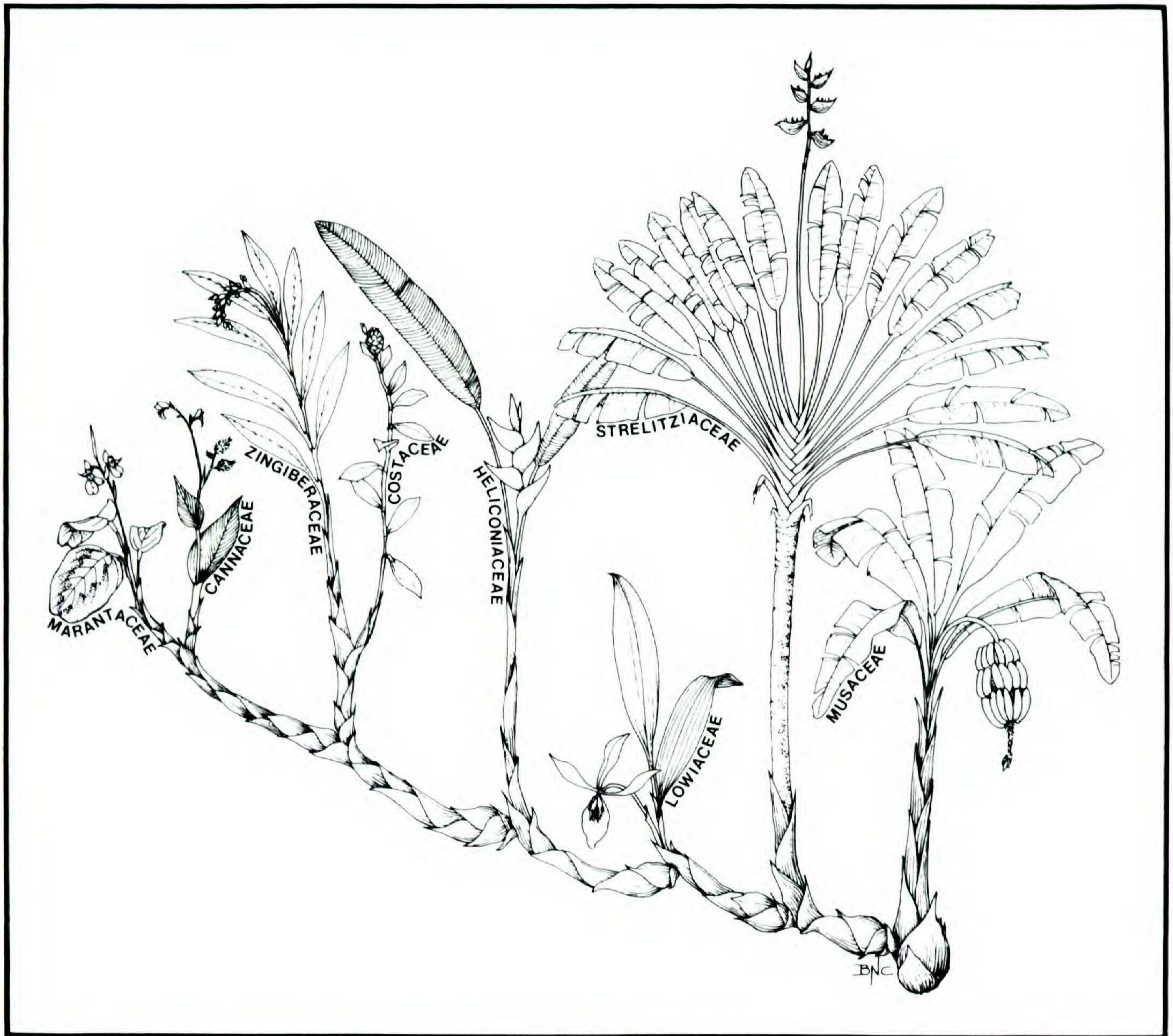
FIGURE 8. "Rhizogram" of the Zingiberales based on Analysis Three and Figure 7.

phyletic groups to be placed at the same rank (here suborders) and listed in the order of the branching sequence, thus reflecting the cladistic relationships without providing a separate categorical rank at each branching point. In the case of the Zingiberales this convention allows the retention of the eight terminal taxa at the rank of family and still provides a classification that exactly reflects the cladistic relationships. The classification depicted in Table 4 lists five new suborders, two new superfamilies, and eight families.

An alternative to erecting new taxa below the ordinal level is simply to list the eight families in order of their branching on the cladogram. Such a classification would cause confusion in reconstructing the relationships of the the families of the ginger group in which the Cannaceae–Marantaceae share a common ancestor not shared by the Zingiberaceae–Costaceae. The problem could be

resolved by accepting the Zingiberaceae–Costaceae as a single family, as done in the past, which would then allow the legitimate listing of the seven families in order of their branching sequence. However, one might counterargue (with less conviction) that the Cannaceae and Marantaceae should also be combined into a single family, something most taxonomists would be reluctant to do.

CONCLUSIONS

The history of the classification of the Zingiberales shows that as information on new characters becomes available, new hypotheses on relationships among the families and taxonomic rank are proposed. In the present investigation, reevaluation of character state distributions and homologies coupled with the methods of phylogenetic systematics has provided a new classification based

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on cladistic hypotheses. However, many phylogenetically useful characters in the Zingiberales remain to be studied carefully, appraised, and verified. Investigations of basic floral and inflorescence anatomy, morphology, and ontogeny, such as currently being carried out by Kirchoff (e.g., 1983a, b, 1986) and Kunze (e.g., 1985, 1986), will provide fundamental data to be incorporated in future analyses. Chemical data are still lacking for most of the families of the Zingiberales. No phylogenetic analysis utilizing molecular characters, such as chloroplast DNA restriction site variation, has yet been attempted on any taxa in the order.

In practice, most taxonomists can ignore the subordinal and superfamilial ranks in the classification proposed here if their goal is identification and placement of taxa only (see Table 5, Fig. 8). However, those biologists wishing to understand the evolution of taxa or characters within the order are dependent upon the phylogenetic information provided by the cladistic classification (Tables 4, 5). For example, as discussed earlier, pollen characters were not used in constructing the cladogram so that their evolution within the order could be inferred from the tree. The pollen wall of most of the families of the Zingiberales is characterized by a highly reduced exine and much-elaborated intine (Erdtman, 1966; Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1982; Kress, 1986). As an exception the Costaceae and Zingiberaceae contain taxa with a well-developed exinous layer in the pollen wall (Punt, 1968; Stone et al., 1981; Kress, 1986). If the distribution of pollen wall features currently known for these families is superimposed on the cladogram of Figure 7, the simplest explanation of wall evolution is obvious. Reduction of the exine layer in the common ancestor of the order accounts for the presence of exineless pollen in six of the eight families. The much-thickened exine layer found in the pollen of the Costaceae and Zingiberaceae is therefore secondarily derived in the common ancestor of these two families, a hypothesis earlier proposed by Stone et al. (1981). The evolutionary explanation may be much more complicated than this, especially because the thickened exine is not found in all genera of the Zingiberaceae (Kress & Stone, unpublished). The important conclusion is that the presence of a thick exine in these families is not indicative of their "primitive" position in the order, but rather the independent evolution of the trait. The diversification of aperture type and the elaboration of the intine layer in the Zingiberales can be investigated in the same manner (Kress & Stone, unpublished). It is hoped that the present phylogeny of the Zingiberales will serve not only as a basis for the classification of taxa in the order, but also as a model for understanding character evolution in the monocotyledons.

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